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PRESENT KNOWLEDGE OF THE SNAKE
ELACHISTODON WESTERMANNI
REINHARDT

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INTRODUCTION

In 1863 Johannes Reinhardt described a peculiar snake belonging to the new genus and species *Elachistodon westermanni*, the specific name referring to the collector, William Westermann, who obtained the initial specimen in Rungpore (Rangpur, see Fig. 1), northeast Bengal. Reinhardt's single specimen was characterized by certain specializations of the integument, by an almost complete absence of teeth, and by certain of the vertebrae bearing hypapophyses which penetrated the esophagus. Comparison with the African snake *Dasypeltis*, long known to be specialized for egg-eating by a similar series of modifications, was inevitable, and Reinhardt came to the conclusion that *Elachistodon* was also an egg-eater. Differences between *Elachistodon* and *Dasypeltis* centered about minuscule grooved teeth and an enlarged row of dorsal scales in the new genus. The presence of the grooved teeth on the posterior aspect of the maxillae suggested the placement of the form in the composite section Opisthoglypha, but Reinhardt pointed to the close similarity between this form and the aglyphous *Dasypeltis* as evidence for the artificiality of this category.

Since 1863 only four additional specimens have been reported and there has been little additional contribution to the morphology or natural history of the species.

A recent study (Gans, 1952) has demonstrated a number of previously undiscussed modifications in *Dasypeltis* and has shown that this genus is much more highly adapted to its very special mode of life than had previously appeared to be the case.

In view of this new knowledge of *Dasypeltis* it was felt that a re-examination of the status of *Elachistodon* would be especially



Fig. 1. The distribution of *Elachistodon westermanni*. Crosses mark the localities where specimens were found.

appropriate at this time. Unfortunately, however, the existing specimens are too few to permit a detailed investigation such as was carried out for *Dasypeltis*. It has, indeed, been possible for one of us (Williams) to make an examination of the specimen in the British Museum and of the osteological preparations from that specimen figured and referred to by Malcolm Smith (1943, p. 403), but the information so derived is suggestive rather than adequate, and it is very evident that further specimens will be needed for thoroughgoing anatomical studies.

This paper, therefore, has two objects. First, it is intended to provide a recapitulation of the existing data on *Elachistodon* in the light of the findings in the genus *Dasypeltis*, and secondly it is desired to reawaken interest in *Elachistodon* in the hope of obtaining the additional specimens upon which the more intensive studies might be based.

HISTORICAL RESUMÉ

The initial specimen was rather fully described by Reinhardt (1863, p. 198), whose careful investigation of its internal anatomy was undertaken because the enlarged vertebral scales of the new form had left him in doubt as to its taxonomic placement. He prepared the tooth-bearing elements of the right side of the skull and one of the mandibles, and checked the condition of the vertebral hypapophyses and their relation to the esophagus without dissecting out the vertebrae or separating them. He found teeth on both palatine and pterygoid as well as teeth and minuscule fangs on the maxilla and described the shape and appearance of the dentary. In comparing *Elachistodon* with *Dasypeltis* he pointed out that in both there were two types of penetrant hypapophyses, though both types in the new form were less well-developed. He figured the palatal and mandibular elements of both genera (see Fig. 4).

The stomach and gullet of the type specimen of *E. westermanni* were found to be filled with an amorphous congealed mass which analysis indicated might be either milk or egg fluid. Though he did not find shell fragments mixed in this mass, Reinhardt speculated on the feeding habits of the animal and appears to have leaned toward the theory that the species was an egg-eater.

Reinhardt also described in detail the squamation of *Elachistodon*, mentioning the very peculiar deep pit on the posterior nasal as well as similarities to *Dasypeltis*. Further details on these and other structural points will be presented in the discussion of the morphology of *E. westermanni*. Reinhardt placed the new genus in the family Raehiodontidae (*sic*).

The next to refer to *Elachistodon* was Günther (1864, p. 444) who mentioned it on Reinhardt's authority only. He suggested that the genus should be separated as a distinct group of colubrids.

Blanford (1875, p. 207) reported the second specimen from Bihar, Purnea (see Fig. 1), and his general description agreed with that of Reinhardt. He suggested that the genus be referred to the Dipsadidae.

Cope (1886, p. 494) considered only the familial assignment of the genus, placing it in the subfamily Dasypeltinae with *Dasypeltis*.

Boulenger in the Fauna of British India (1890, p. 362) placed the genus in the Opisthoglypha, Dipsadinae, next to *Dipsas*. He stated that he had not been able to examine specimens but from the key (pp. 356-357) it appears that the assignment was based on the grooved teeth, the enlarged vertebral shields and the elliptically vertical pupil. He also referred to esophageal teeth capped with enamel.

Sclater (1891, p. 48) in listing the snakes in the Indian Museum recorded a specimen from Bengal which seems to have been that earlier recorded by Blanford. He placed it in the Dipsadinae.

In the Catalogue of the Snakes of the British Museum, volume 3, Boulenger (1896, p. 263) erected the subfamily Elachistodontinae of the Colubridae with the single genus *Elachistodon*. He regarded this as the opisthoglyphous analogue of the aglyphous Rachiodontinae. His description of the subfamily mentions pterygoid teeth.

The next record is that of Wall (1913, p. 400) who reported a new specimen from the Jalpaiguri district (see Fig. 1) and published a detailed comparison of the three specimens then known. He did not give the sex of the third specimen (it is, however, the female described again by M. Smith, 1943) but did cast doubt on the presence of pterygoid teeth. His later 'Handlist' (1923, p. 878) did not contain any new data.

In a serialized discussion of the snakes of northern Bengal and Sikkim, Shaw, Shebbeare and Barker (1941, p. 65) list the specimens known to them. In addition to the original Rangpur specimen in the Museum at Copenhagen they cite a second from Purnea (the Blanford specimen) in the Indian Museum at that time. The specimen obtained by Travers at Jalpaiguri (Wall, 1913) was stated to be in the Bombay Museum (it is now in the British Museum), while the then whereabouts of two addi-

tional specimens obtained by Travers at Baradighi¹ appeared to be unknown.

Malcolm Smith (1943, p. 403) redescribed the genus and removed it from the Elachistodontinae to the Dasypeltinae. He presented the first published figures of the modified vertebrae and also refigured the palatal bones. Pterygoid teeth are not mentioned in his text or shown in his figure.

Smith and Bellairs (1947, p. 362) mention only that the Harderian gland is enlarged in this form as in *Dasypeltis*.

MORPHOLOGY

General

The following condensed diagnosis is designed to aid identification of specimens. For this reason it follows the summary presented by Smith (1943, p. 404) with only minor modifications.

Head fairly distinct from neck; eye large with vertically elliptical pupil (round *vide* Reinhardt); a large pit in the posterior part of the nasal shield. Body moderately elongate, feebly compressed. Tail short, subcaudals paired.

Internasals as large as prefrontals; frontal large, longer than its distance from the end of the snout; nasal large; 1 small preocular, the loreal below it entering orbit; two postoculars; two long anterior temporals; 6 or 7 supralabials, the third and fourth touching the eye; 2 pairs of sublinguals. Scales smooth, in 15 rows, 19 on the neck, the vertebral series much enlarged, hexagonal. Anal single. Ventrals 208-217. Caudals 59-65.

Above, dark olive brown to blackish, the vertebral scales yellowish-white, except at their outer margins, forming a light vertebral stripe extending the whole length of the body; sides spotted or flecked with the same color; whitish below, the outer margins of the ventrals and adjacent rows of scales edged with brown; a yellow stripe along the top of the head from the snout to the angle of the mouth, passing above the eye; an angular bar or spot on the nape; lips yellow.

♀ 784 mm. (670 + 114 mm.). Ventrals 217. Caudals 59. Rungpore, Bengal. Copenhagen Museum (Reinhardt).

¹ We have been unable to find Baradighi on any map, but the Indian Consular Office in New York has very kindly informed us that there is a railroad station by that name about 30 miles north of Calcutta.

- ♀ 800 mm. (670 + 130 mm.) *fide* Smith, (762 mm. [635 + 127 mm.] *fide* Wall). Ventrals 213 (210). Caudals 62 (64). Near Mal, Jalpaiguri District. Formerly Bombay Museum, now British Museum (Natural History).
- ? 222 mm. (186 + 35.7 mm.), Ventrals 208. Caudals 63. Bihar, Purnea. Indian Museum (Blanford).

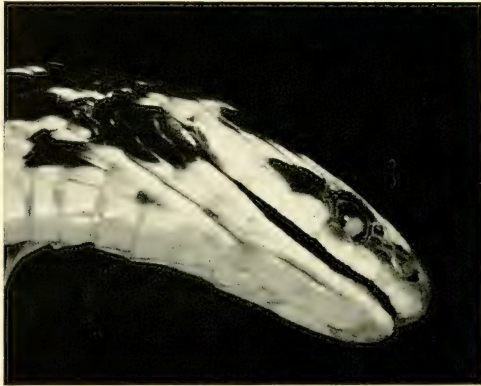


Fig. 2. *E. westermanni*. Oblique view of the head of the British Museum specimen to show the expansion lines between the lower labials at the angle of the mouth.

Squamation of Head and Neck

The most significant integumentary similarities between *Elachistodon* and *Dasypeltis* are the structure and arrangement of the gular and cheek scales. This similarity was already pointed out by Reinhardt who, however, did not know the function of the parallel structures. The fact that in *Dasypeltis* these gular and cheek specializations have been definitely shown to be elaborate adaptations for egg-eating suggests that the possession of similar structures by *Elachistodon* is correlated with similar habits.

In both *Elachistodon* and *Dasypeltis* there are two pairs of sublinguals closely joined and lacking any evidence of the median groove that in most snakes provides for expansion. In *Dasypeltis*

there are no true gular scales at all, while in *Elachistodon* there is but one row of these. In both of these forms the sublinguals are so rigidly tied in that expansion of the chin region can only take place along the angle of the mouth during ingestion. In *Dasypeltis* this expansion is made possible by the presence of extremely distensible skin between the scales of this region. The last labials have also been rearranged to form the first scales of the lowest lateral rows. The same condition is also the case in *Elachistodon*, and the resulting lines of expansion are clearly seen in Figure 2. Such a specialization, the value of which is probably solely restricted to egg-eating, would tend to furnish additional evidence for the idea that other described modifications of *Elachistodon* are adaptations to this habit.

A possibly significant point of difference between *Elachistodon* and *Dasypeltis* is the presence in the form of a large pit on the posterior part of each nasal shield. The function of similar pits in the Crotalidae as well as in certain species of Pythonidae has been determined to be that of a thermosensitive range-finder (Noble and Schmidt, 1937), and it is known that similar structures of as yet uninvestigated function exist in other forms. In *Elachistodon* nothing is known of the function of the pits.

Squamation of the Posterior Body

The enlargement of the vertebral series of dorsal scales characteristic of *Elachistodon* is a feature also found in a large number of dipsadine and other snakes but not in *Dasypeltis*. Little is known about the function of this enlargement although Peters (MS 1952, p. 27) has speculated on its relation to the arboreal habits of the dipsadines. He believes that in conjunction with the extreme lateral flattening of the body it might impart a stiffening effect. He offers the analogy of an I-beam, and suggests that the enlargement of the vertebrae might permit the unusual horizontal rigidity and extension observed in climbing members of the Dipsadinae. We cite the suggestion here without passing judgment upon its applicability to *Elachistodon*, which shows but feeble lateral compression.

It is also to be noted that the scales of *Elachistodon* are smooth while those of *Dasypeltis* are strongly keeled. This character is, however, of little value at the generic level or above, in view of

the number of cases in snakes in which it shows intrageneric variation.

Elachistodon exhibits no trace of the size reduction, angling and serration exhibited by the second to sixth rows of dorsal scales in *Dasypeltis*. Except for the vertebral row all the dorsals are uniform in size and character.

Soft Tissues of the Head

No published observations are available on gum structure. Examination of the British Museum specimen indicated that the gum ridges are probably covered with a somewhat less convoluted mass of tissue than are those of *Dasypeltis*.

Smith and Bellairs (1947, p. 362) have noted that the Harderian gland is notably enlarged in *Elachistodon* paralleling the condition in *Dasypeltis*.

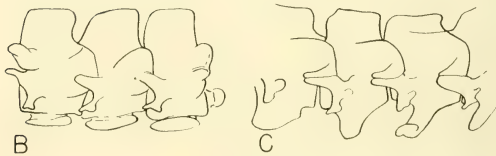
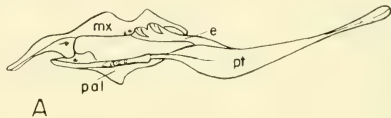


Fig. 3. *E. westermanni*. A, Palatal bones; B, anterior hypapophysial vertebrae; C, posterior hypapophysial vertebrae. Abbreviations: *e*, ectopterygoid; *mx*, maxillary; *pal*, palatine; *pt*, pterygoid. After Malcolm Smith (1943).

Skull

To the best of our knowledge no complete skull has ever been prepared. The palatal elements have been figured by Smith (1943) (see Fig. 3, A). A check of the material by one of

us (Williams) found the figures accurate in all particulars including the fact that pterygoid teeth (described and illustrated by Reinhardt in the Copenhagen specimen) are not to be seen.

Comparison with the homologous elements in *Dasypeltis* indicates few differences beyond the presence of the relatively enlarged grooved teeth on the posterior aspect of the maxilla in *Elachistodon*. This portion of that bone is also somewhat more strongly developed and there are general though minor differences in the relative proportions of the various structures. The union between palatine and maxillary may be somewhat weaker than the corresponding articulation in *Dasypeltis*. The wing-shaped process of the palatine is much abbreviated though this process is shown as greatly extended in Reinhardt's drawing. These bones are, however, very fragile, and it may be possible that some of the apparent differences may be traced to the method by which these elements were cleaned. The similarities seen lead us to the conclusion that the palatal elements of *Elachistodon* are as rigidly joined as those of *Dasypeltis*.

The dentitional formulae are as follows: Maxilla edentulous except for two small teeth followed by two larger grooved teeth; palatine with four minute teeth in its center; pterygoid — according to Reinhardt — with three extremely minute teeth. Wall (1913) and Smith (1943) — both treating of the specimen from Jalpaiguri — do not refer to pterygoid teeth. The dentary has eight to twelve teeth diminishing in size posteriorly.

Reinhardt has figured and described the anterior end of the mandible for both *Elachistodon* and *Dasypeltis*. The appearance of the element in *Elachistodon* is very strange, and since the figure of the same element in *Dasypeltis* bears very little resemblance to actual specimens seen by us, we do not care to comment further in this matter (see Fig. 4).

Vertebral Column and Esophagus

There are certain rough similarities in the appearance of the anterior vertebrae (hypapophysials) in the two forms. In both there are two basic types of hypapophyses — anterior and posterior, but in *Dasypeltis* some of the anterior hypapophyses undergo considerable ontogenetic variation so that it is best to distinguish anterior, intermediate, and posterior types. It is not known

whether similar ontogenetic variation is found in *Elachistodon*. For the latter genus, therefore, these comments must of necessity be restricted to the modified vertebrae of the adults.

In *Dasypeltis* the anterior hypapophyses are little modified. They are of the "normal" squarish shape with only their ventral edges enlarged into sled-like runners. The egg glides along these runners during ingestion, but the runners do not serve any cutting or sawing function. The egg is pierced by the elongate, spiniform, forward pointed hypapophyses of the posterior series, which penetrate the esophagus in all specimens (Gans, 1952, p. 236). After the shell has been broken, the heavy rounded boss-like hypapophyses of the intermediate series transmit a crushing force to the egg shell and fold this, while the egg contents are being squeezed into the stomach through the esophageal valve. The forces involved in this action are sizable, and for this reason the articulating surfaces of the neural arches are greatly expanded, the pre- and postzygapophyses being laterally displaced and extended by spiniform processes. This offers additional surface for the action of the dorsal musculature which is kept from lateral slippage by the confining inclination of the surfaces of attachment.

The intermediate and some of the anterior hypapophyses are penetrant in adults of *Dasypeltis*, but this character shows considerable variation in juveniles. There is also evidence that some seasonal variation of this character may occur in adult specimens as well.

In *Elachistodon* nothing appears to be recorded about the hypapophysial vertebrae immediately posterior to the cervicals, and these have never been figured. Perhaps it may be assumed that they are of "normal" appearance, possibly performing the same function as do the homologous structures in *Dasypeltis*. There is no record as to the number of these "unmodified" vertebrae, though Smith (1943, p. 403) states that the modified hypapophyses start opposite the tenth ventral shield.

The amount of skeletal preparation which has been done for this region is very limited. Reinhardt (1863, footnote to p. 202) stated that he had not skeletonized but rather examined the vertebral column *in situ*. Smith figures two short sections of three vertebrae each (Fig. 3, B and C). One of us (Williams)



A



B



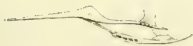
C



D



E



F



G

Fig. 4. Plate from the original description by Reinhardt. *A, B, C*, Dorsal, ventral and side views of the head of *E. westermanni*; *D*, palatal bones of *E. westermanni*; *E*, dentary of *E. westermanni*; *F*, palatal bones of *Dasypeltis scaber*; *G*, mandible of *Dasypeltis scaber*.

has examined these vertebrae, and the following statement is based on this examination.

The more anterior of the prepared and figured hypapophyses are very strange in appearance. Bosses are present as in the intermediate hypapophyses of the African form, but they are not as closely integrated with the base of the centrum. They are instead mounted on a pedicel beyond which they extend both anteriorly and posteriorly. The vertebrae bearing these hypapophyses are relatively undifferentiated. No extension or inclination of the zygapophysial surfaces is apparent.

In some ways the anterior hypapophyses of *Elachistodon* are reminiscent of stages in the ontogeny of the intermediate hypapophyses in *Dasypeltis*, though the mounting on a pedicel suggests that they may be specialized in a different direction. Reinhardt (1863, p. 203) stated that there were nine such anterior hypapophyses, while Smith (1943, p. 403) counted eighteen all of which projected through longitudinal slits into the esophagus. Both authors believed that these are cutting instruments, which hardly seems likely in view of the findings in *Dasypeltis*.

Compared to the posteriormost hypapophyses in *Dasypeltis* which are such highly effective tools, these same elements in *Elachistodon* seem even less modified than the anterior hypapophyses. In *Elachistodon* the hindmost hypapophyses are block-shaped spines whose major specialization lies in the fact that they are directed forward rather than backward. They most nearly resemble the hypapophyses of several of the species of *Elaphe* recently mentioned as being specialized for egg-eating (Gans and Oshima, 1952, p. 15), but they also resemble those hypapophysials of very young *Dasypeltis* that are transitional between the intermediate and the posterior series.

Reinhardt speaks of thirteen of the posterior type hypapophyses in *Elachistodon*, with only the first ten penetrating the esophagus, while Smith mentions eight of these structures, none penetrating the esophagus. Smith's observation would of course be in strong contrast to the findings in *Dasypeltis*, and the contradiction in observations here makes it quite clear that the egg-eating habits of this form will have to undergo a separate analysis to determine the extent to which parallelism in function exists, and to explore the differences.

In spite of this, it may be stated that all indications exist that eggs are opened by *Elachistodon* in a manner similar to that employed by *Dasyplettis* and *Elaphe climacophora*, i.e. by exerting a force concentrated by the processes of the vertebrae.

A comment may be made on Smith's Figure C (our Fig. 3 C). The third figured hypapophysial carries a hypapophysis with what appears to be a shovel-shaped tip. While the drawing is entirely accurate, its two-dimensional nature does not do the subject justice, as this tip is actually deformed into a hook in the horizontal plane in a most peculiar manner. The asymmetry and other features of the structure make it obvious that this is merely an individual aberration of no adaptive or other significance. Similar variations occur on the hypapophyses of a number of other oophagous and non-oophagous species of snakes examined by us.

Finally it may be well to mention that the hypapophyses in *Elachistodon* are formed of very dense bone only and do not consist of enamel as stated by various authors. While it has not been possible to undertake histological studies for this form, detailed and repeated investigations have shown this to be true for *Dasyplettis* (Gans, 1952; Gans and Oshima, 1952), and no evidence exists which might permit the contrary conclusion in *Elachistodon*.

BIOLOGY

No specimen of *Elachistodon* has ever been kept in captivity and there exist no notes on habits or habitats in the wild. With the exception of Reinhardt's specimen which had egg yolk (?) in its stomach, no other observations on stomach contents have been published. The consensus of the literature (based on no direct evidence) is that the form eats "eggs but not exclusively." The presence of grooved teeth and the nasal pit suggest that the species may feed also on live and homoiothermous prey.

The only other item of interest concerns breeding habits. The type was a gravid female, containing seven (40 x 11 mm.) eggs (Reinhardt, 1863, p. 210). None of these contained embryos although they were already covered with a relatively heavy shell. This would indicate that the species is oviparous as is also true for *Dasyplettis*.

Comparison of *Elachistodon* and *Dasypeltis*

The following tables sum up the more important similarities and differences — at present known — of the two genera.

Points of Similarity

Sublingual shields fused, mental groove absent; special provision for expansion of the skin along the angle of the mouth and in the cheek region; Harderian gland much enlarged; palatal elements modified, largely edentulous, with teeth present only on the posterior aspects of maxilla and palatine; ? upper jaw elements rigidly tied together; teeth on posterior aspect of dentary only; a loose articulation between dentary and compound bone. Vertebral hypapophyses modified, some penetrating the esophagus; anterior hypapophyses generally rounded, with sledge-like runners or bosses; posterior hypapophyses developed as forward-pointing spines; oviparous.

Points of Difference

<i>Dasypeltis</i>	<i>Elachistodon</i>
Nasal pit absent	Nasal pit present
No gulars	One row of gulars
Scales strongly keeled	Scales smooth
Vertebral scale row subequal to dorsals	Vertebral scale row enlarged
Some lateral rows with scales reduced in size, inclined and with serrate keels	All lateral rows with scales of equal size
Maxillary teeth minute and equal	1-2 enlarged grooved teeth on rear of maxilla
Intermediate hypapophyses heavy, rounded, boss-like, closely applied to centra	Bosses of hypapophyses separated by constriction from centrum, i.e. mounted on pedicel
Posterior hypapophyses bear sharply pointed spines and penetrate esophagus	Posterior hypapophyses much less strongly developed, ? no penetration
Elliptical pupil	? Round pupil (<i>vide</i> Reinhardt)
No pterygoid teeth	? Pterygoid teeth (<i>vide</i> Reinhardt)

Inspection of the above lists reveals that the similarities between the two forms are primarily those of structures which in *Dasypeltis* are known to be connected with egg ingestion. Many of the differences are at a level generally associated with a generic separation, while only the nasal pit and the grooved fangs might indicate a higher level of difference.

It has been suggested that *Elachistodon* may be a less specialized form than *Dasypeltis* but derived from a common ancestral stock that may have been opisthoglyph or even proteroglyph. According to this, greater specialization in *Dasypeltis* has brought about the total loss of the fangs as well as the additional modifications exhibited by this genus. Analysis of the relationships of the genus *Elachistodon* may indeed yield evidence shedding light on the general problem of the origin of the opisthoglyphs.

Beyond the two genera which have been compared here, analysis will have to be carried forward for the various other forms known or suspected to be specialized egg-eaters before it will be possible to determine whether we are dealing with a single series or a set of parallel modifications in separate lines.

It is to be borne in mind that we have here reported for the most part the observations of others and have had little opportunity to check these against actual specimens. It may well be that careful examination of a large series of specimens would force a revision of our understanding of the morphology of *Elachistodon*. This is particularly likely in view of the high amount of variation exhibited by the much better known *Dasypeltis*. The many points of difference noted from the scanty literature testify only too clearly that a similarly high amount of variation is present in *Elachistodon*. It would obviously be dangerous to speculate at this time on the larger problems offered by the Indian genus.

In view of this dearth of knowledge and the high interest of the Indian genus, the authors wish to urge local zoologists or anyone whose work may take him into the range of this form to secure us specimens. Any such material may be sent to either of our institutions. Credit will of course be given in any subsequent reports.

Acknowledgments. Our thanks are due to a considerable num-

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